

THE WILSON BULLETIN

A QUARTERLY JOURNAL OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 117, NO. 2

June 2005

PAGES 113–210

Wilson Bulletin 117(2):113–127, 2005

A NEW SPECIES OF GNATCATCHER FROM WHITE-SAND FORESTS OF NORTHERN AMAZONIAN PERU WITH REVISION OF THE *POLIOPTILA GUIANENSIS* COMPLEX

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ABSTRACT.—We describe a new species of gnatcatcher, *Poliioptila clementsi*, from white-sand (*varillal*) forest at the Allpahuayo-Mishana National Reserve, about 25 km by road west of Iquitos, Peru. To date, the new species is known only from the reserve, and is rare even there. Comparisons of morphological and vocal characters confirm that it is a member of the *Poliioptila guianensis* complex, which comprises at least three poorly known, allopatric taxa ranging from the Guianas and the Rio Negro region through much of Amazonia south of the Amazon River. Roughly equivalent levels of phenotypic differentiation are documented for all taxa east of the Andes, including the new species. In consideration of the fact that some other species complexes in the genus comprise sister taxa showing lower levels of phenotypic differentiation, both morphologically and vocally, we recommend that *Poliioptila guianensis*, *P. facilis*, and *P. paraensis* henceforth be recognized as separate species. Received 4 June 2004, accepted 1 March 2005.

RESUMEN.—Describimos una nueva especie de perla, *Poliioptila clementsi*, del bosque de arena blanca (*varillal*) de la Reserva Nacional Allpahuayo-Mishana, a 25 km por carretera al oeste de Iquitos, Perú. Hasta la fecha, la nueva especie es conocida solamente de la reserva, y es rara incluso allí. Comparaciones de caracteres morfológicos y vocales confirman que es un miembro del complejo *Poliioptila guianensis*, que comprende al menos tres taxones alopatricos muy poco conocidos, que se extienden desde la región de las Guayanas y el Rio Negro a través de gran parte de la Amazonía al sur del Rio Amazonas. Son documentados niveles aproximadamente equivalentes de diferenciación fenotípica para todos los taxones al este de los Andes, incluyendo la nueva especie. En consideración al hecho de que algunos otros complejos de especies en el género comprenden taxones hermanos que muestran una diferenciación fenotípica menos marcada, tanto morfológica como vocal, recomendamos que de aquí en adelante *Poliioptila guianensis*, *P. facilis*, y *P. paraensis* sean reconocidas como especies separadas.

The recent discovery of two species of birds new to science (Ancient Antwren, *Herp-silochmus gentryi* and Allpahuayo Antbird, *Percnostola arenarum*) and several others previously unknown from Peru in the white-sand forests of northern Loreto has revealed the presence of an avifauna with close Guianan

affinities extending westward from the Iquitos area into eastern Ecuador (Alvarez and Whitney 2003). In the early stages of recognizing this pattern, we focused fieldwork on searches for additional species we predicted to have a high likelihood of occurrence in the various white-sand forest types in this region. Among these was *Poliioptila guianensis* (Guianan Gnatcatcher), a poorly known canopy insectivore represented by about 30 specimens in the world. Its nearest documented point of occurrence lay some 800 km distant along the upper Rio Negro in Brazil near São Gabriel da Cachoeira (BMW pers. obs.).

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On 9 September 1997, JAA found what appeared to be *Poliioptila guianensis* in tall, white-sand forest in the proposed Allpahuayo-Mishana Reserve outside Iquitos on the road to Nauta. He noted, however, that the birds' songs differed distinctly from BMW's recordings from Brazil. In subsequent years, we obtained three specimens and a good sample of recordings of the songs and calls of this gnatcatcher, which appears to have a highly restricted distribution, even within the reserve. After comparing our specimens and sound recordings with those of all Neotropical gnatcatcher species, especially *P. guianensis* from diverse points in its distribution, we are convinced that the Iquitos-area birds are most closely related to *P. guianensis*, and would best be described as a new species, which we propose to name:

Poliioptila clementsi sp. nov.

Iquitos Gnatcatcher

Perlita de Iquitos

Holotype.—Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru, No. 21113; male (skull unossified) from the Zona Reservada Allpahuayo-Mishana, 03° 55' S, 73° 29' W, south bank of Rio Nanay, approximately 25 km wsw of Iquitos, Department of Loreto, Peru; 150 m elevation; 15 December 1998; collected by JAA. Voice specimen of an accompanying individual is archived at the Macaulay Library of Natural Sounds (MLNS), Cornell Laboratory of Ornithology, Ithaca, New York; LNS 120444. A sample of liver tissue was preserved (Alvarez No. 1.12.98) and will be accessioned at the Louisiana State University Museum of Natural Science (LSUMZ) once it is legally exported from Peru.

Diagnosis of Poliioptila clementsi sp. nov.—A typical member of *Poliioptila* (*sensu* Ridgway 1904:710–711), including a thin black bill and graduated tail, with narrow rectrices bearing conspicuous white on the outer three pairs but none on the three central pairs. The following pertains only to males, as we have no specimens of female *P. clementsi*. Readily distinguished from all congeners except *P. guianensis*, from which it differs by its significantly longer bill (mean 12.1 versus 11.4 mm; culmen from base at skull). On a taxon-

by-taxon basis, differs from *P. g. guianensis* by uniformly gray throat and breast (instead of throat conspicuously paler than breast) and presence of black bases on outer and penultimate pairs of rectrices, with third pair mostly black (instead of three outer pairs entirely, or almost entirely, white); from *P. g. facilis* by presence of a conspicuous, broken white eye-ring (lacking in *P. g. facilis*) and greater extent of white on outer rectrices (approximately basal 1/3–1/2 black in *P. g. facilis*); from *P. g. paraensis* by generally darker and more bluish-gray plumage, and greater extent of white on outer rectrices (approximately basal 1/3–1/2 black in *P. g. paraensis*). Readily distinguished from *P. schistaceigula*, the purported closest relative of *P. guianensis* (Zimmer 1942), by much paler plumage overall and somewhat longer tail with extensive white (rectrices essentially all black in male *P. schistaceigula*). Males of all other species of *Poliioptila* have discrete areas of black on the head (ranging from streaks to extensive caps) in definitive alternate plumage, among other differences.

Diagnosis of voice.—Loudsong structurally similar to, but immediately distinguished from, all forms of *P. guianensis* by presence of sharp, “inverted chevron-shaped” introductory notes (virtually always three of these) delivered slowly enough to be counted in the field, followed by a series of evenly spaced notes delivered at a faster pace than by any of the taxa of *P. guianensis*. The loudsong of *P. schistaceigula* is a variable set of notes lacking coherent, repetitive structure in series, and is thus very different; other species of Neotropical gnatcatchers are widely and variably divergent in both songs and calls.

Distribution.—Known only from tall, *Carai-pa*-dominated *varillal* forest (see Habitat and behavior section below) at the type locality (the Reserva Nacional Allpahuayo-Mishana) just west of Iquitos, Department of Loreto, Peru.

Description of holotype.—See color frontispiece. Capitalized color designations (corresponding number in parentheses) from Smithe (1975). Rictal bristles present, inconspicuous. Upperparts from base of bill to uppertail coverts, sides of head, and upperwing coverts essentially uniform and closest to Dark Neutral Gray (83), in some lights appearing slightly more bluish, toward Plumbeous (78). Head

lacking discrete areas of black or white except for a narrow, white eye-ring, slightly broken at front and back edges. Throat and breast, including some posterior extension to sides, slightly paler than upperparts (lightest at the lower breast/upper belly), Medium to Light Neutral Gray (84–85). Belly and undertail coverts white. Primaries and secondaries closest to Blackish Neutral Gray (82), outer vanes of primaries finely edged with same gray as upperparts, inner vanes narrowly edged whitish. Alula and smaller, overlying feather blackish with thin whitish margin on outer vane; primary coverts same blackish but lacking whitish margins. Underwing coverts white, the tiny coverts at base of outer primaries and at bend of wing with dark gray centers and whitish tips. Tail full (12 complete rectrices) and unabraded, distinctly graduated. Three inner pairs entirely blackish. Black/white pattern on No. 4 and No. 5 differs on left and right sides of the bird, the right side having somewhat more white, especially on the outer vanes. Rectrix No. 4 mostly blackish with white tip (about 5 mm on inner vanes, to about 10 mm on outer vanes); No. 5 mostly white with approximately basal 1/4–1/3 blackish, on the inner vane extending posteriorly from the rachis to the feather margin in a diagonal strip to invade the white region to within about 15 mm of the tip on the right feather and to within 12 mm of the tip on the left feather. Outer rectrices (pair No. 6) white with about basal 1/5 of outer vane blackish, basal 1/3 of inner vane blackish and showing same diagonal, posterior extension described for No. 5 only to a lesser degree. Rectrices show same pattern on ventral and dorsal surfaces except that No. 4 appears wholly blackish (like the two central pairs, no white tip visible) when viewed from above. Soft parts in life: iris brown, maxilla black with paler commissure, mandible grayish-horn, legs and feet bluish-gray, soles of feet whitish. MUSM 21113 was selected for the holotype because it is in the best condition of the three available specimens, and has a complete and fully grown tail. Its cranium was clear and unossified; thus, it may be a juvenile.

Measurements of holotype.—Wing (chord) 45.4 mm, tail 45.8 mm, culmen from base (at skull) 12.7 mm, bill width at anterior edge of nares 2.3 mm, tarsus 15.3 mm, mass 6.0 g.

Specimens examined.—Only specimens that were measured are listed. Specimens of all other *Polioptila* species in South America were compared superficially. The sample below was restricted to *P. guianensis* and *P. schistaceigula*, the presumed closest relatives of *P. clements*. Some standard measurements of these specimens, with sample sizes, are presented in Table 1.

Polioptila clements sp. nov.: Peru: Loreto, Allpahuayo-Mishana area, three males (MUSM 21111, 21112, 21113).

Polioptila guianensis guianensis (eight males, four females): French Guiana: Tama-noir, Mana River, two males (Carnegie Museum of Natural History [CM] 61912, 61923, paratypes); Oyapock, Pied Saut, three males, one female (CM 64921, 65782, 65783; American Museum of Natural History [AMNH] 233949, paratypes). Suriname: Maroni District, Negerkreek, one female (AMNH 461499). Guyana: Potaro Landing, one female (AMNH 126034); Iwokrama Forest Reserve, one male, one female (Academy of Natural Sciences [ANSP] 188049, 188050). Brazil: Amazonas, north of Manaus, two males (Museu Paraense Emílio Goeldi [MPEG] 53260, 53261).

Polioptila guianensis facilis (five males, one female): Venezuela: Amazonas, Solano, one male (AMNH 433542, holotype); Mt. Duida, Rio Pescado, one male (AMNH 275037, paratype). Brazil: Amazonas, Mt. Curucuryari, one female (AMNH 311254, paratype); Parque Nacional do Jaú, two males (MPEG 50678, 50679); Roraima, Colônia do Apiaú, one male (Field Museum of Natural History [FMNH] 344215).

Polioptila guianensis paraensis (two males, three females, one sex unknown): Brazil: Pará, Município Capim, one male, one female (Museu de Zoologia da Universidade de São Paulo [MZUSP] 45687, 45693); Caxiricatuba, one male, one female (AMNH 287648, 287649); Amazonas, Borba, Rio Mapiá Grande, one sex unknown (MPEG 53263); Rondônia, Cachoeira Nazaré, one female (FMNH 344216).

Polioptila schistaceigula (one male, three females): Colombia: Cauca, two females (AMNH 107540, 133935). Ecuador: Esmeraldas, Cachabí, one male (AMNH 502979, holotype); Pichincha, one female (LSUMZ 162122).

TABLE 1. Some standard measurements of *Poliophtila clementsii* sp. nov., *P. guianensis* (three subspecies), and *P. schistaceigula* from northern South America. Values are means (range, n).

Taxon	Bill width (mm) ^a	Culmen (mm) ^b	Wing chord (mm) ^c	Tail (mm)	Body mass (g)
<i>P. clementsii</i>					
Male	2.4 (2.3–2.5, 3)	12.1 (11.7–12.7, 3)	44.3 (43.5–45.4, 3)	46.6 (45.8–47.6, 3)	5.6 (5.1–6.0, 3)
<i>P. g. guianensis</i>					
Male	2.3 (2.2–2.5, 8)	11.5 (10.9–12.0, 6)	46.6 (44.5–49.0, 8)	46.5 (44.1–48.9, 4)	6.2 (5.4–6.9, 3)
Female	2.4 (2.3–2.4, 2)	11.4 (11.1–11.6, 3)	46.0 (45.5–46.6, 2)	43.9 (1)	6.0 (1)
<i>P. g. facilis</i>					
Male	2.5 (2.3–2.7, 5)	11.4 (11.1–11.7, 5)	45.3 (44.8–45.7, 5)	46.3 (45.2–47.4, 5)	5.9 (5.5–6.5, 3)
Female	—	11.8 (1)	44.2 (1)	46.3 (1)	—
<i>P. g. paraensis</i>					
Male	2.5 (1)	12.0 (11.9–12.0, 2)	45.0 (44.5–45.5, 2)	50.3 (48.8–51.8, 2)	—
Female	2.5 (2.3–2.7, 2)	11.4 (10.8–11.9, 3)	45.5 (43.0–49.0, 3)	48.6 (47.2–50.1, 3)	5.8 (1)
Sex unknown	2.5 (1)	10.8 (1)	43.0 (1)	48.9 (1)	5.9 (1)
<i>P. schistaceigula</i>					
Male	2.5 (1)	13.7 (1)	46.9 (1)	42.4 (1)	—
Female	2.5 (2.4–2.5, 3)	12.3 (11.9–12.7, 3)	44.4 (43.7–45.6, 3)	41.6 (38.6–43.4, 3)	6.0 (1)

^a Measured at anterior edge of nares.^b Measured from base at skull.^c Both wings usually measured; longer measurement included here.

Tape recordings examined.—Sample sizes are number of individuals recorded; 1–4 vocalizations of each type were measured for each individual (means and ranges for samples are presented in Table 2). *Poliophtila clementsii* sp. nov.: Peru: Loreto, Allpahuayo-Mishana area, 10 loudsong (9 JAA, 1 BMW), 8 calls (7 JAA, 1 BMW). *Poliophtila guianensis guianensis*: Brazil: Amazonas, north of Manaus, two loudsong, two calls (all L. Naka). *Poliophtila guianensis facilis*: Brazil: Amazonas, near São Gabriel da Cachoeira, seven loudsong (4 BMW, 3 K. J. Zimmer), four calls (K. J. Zimmer). *Poliophtila guianensis paraensis*: Brazil: Pará, Caxiuanã National

Forest, six loudsong (5 BMW, 1 C. A. Marantz); Serra dos Carajás, two loudsong, one call (all BMW); Novo Progresso, one loudsong (J. F. Pacheco); Vila Braga, one loudsong (BMW); Jacareacanga, one loudsong (BMW); Amazonas, Rio Sucundurí, one loudsong (BMW); Mato Grosso, Comodoro, one loudsong, four calls (A. Whittaker). Two of the *P. clementsii* were collected subsequent to tape recording (the third specimen was in the company of a bird that was tape recorded); none of the *P. guianensis* was collected.

Biochemical specimens.—Tissues were saved in DMSO (dimethylsulfoxide) buffer solution (to be deposited at LSUMZ once it is

TABLE 2. Some measurements of *Poliophtila clementsii* and *P. guianensis* (three subspecies) loudsongs from northern South America. Values are means (range; no. of vocalizations, no. of individuals).^a

Taxon	Pace of first three notes	Pace without first three notes	ΔPF^b
<i>P. clementsii</i>	0.14 (0.13–0.16; 33, 10)	0.07 (0.06–0.07; 33, 10)	1.98 (1.75–2.30; 33, 10)
<i>P. g. guianensis</i> ^c	0.12 (0.12–0.13; 2, 2)	0.14 (0.13–0.15; 2, 2)	0.47 (0.31–0.63; 2, 2)
<i>P. g. facilis</i> ^d	0.08 (0.07–0.10; 20, 6)	0.13 (0.12–0.14; 19, 6)	0.94 (0.52–2.33; 20, 6)
<i>P. g. paraensis</i> ^e	0.09 (0.07–0.10; 15, 6)	0.11 (0.09–0.12; 15, 6)	0.37 (0.21–0.61; 15, 6)

^a Means and ranges reflect combined measures of the number of birds recorded. All measurements taken at peaks of notes.^b Change in peak frequency from first to last note.^c Sample from near Manaus, Amazonas, Brazil.^d Sample includes both banks of upper Rio Negro, Amazonas, Brazil.^e Sample from Caxiuanã National Forest, Pará, Brazil.

exported from Peru) for all three of the specimens of *Poliioptila clementsii*. We know of four tissue samples of other members of the *P. guianensis* complex (see Specimens examined listed above): ANSP 188050 is tissue number ANSP 8192; ANSP 188049 is tissue number ANSP 8307; and MPEG 53260 and 53261 are tissue numbers LSUMZ B-20230 and B-20266, respectively.

Etymology.—We are pleased to name this new species in honor of James F. Clements in recognition of his generous and forward-thinking contribution to preserving the Allpahuayo-Mishana National Reserve, and the habitat of *Poliioptila clementsii* in particular. Jim's influence on the world of birding, primarily through his carefully maintained world checklist of birds, has been enormous and has sparked the interest of many birders to travel to remote places in search of rarities like the Iquitos Gnatcatcher. The money generated by the activities of birders has ever-growing importance in supporting local economies, and it encourages government authorities to recognize the economic value of ecosystem preservation.

REMARKS

Variation in the type series.—The type series consists of the three male specimens listed above, all of which have essentially unossified skulls and are probably juveniles. One of them (MUSM 21111) was one of four individuals foraging together in a mixed-species flock and was thought to have been giving food-begging calls. Plumage of this specimen and MUSM 21112 closely match the description of the holotype. The holotype and MUSM 21111 were collected in mid-December, and both showed contour molt but no molt in the flight feathers. MUSM 21112, taken in early April, also showed contour molt and had half-grown central rectrices with the right outer rectrix barely emergent from its sheath. All specimens show the slight variation in pattern of black and white on the rectrices described for the holotype.

Some variation in iris color can be surmised from the specimen labels. The holotype was "brown," MUSM 21111 was recorded as "grayish-brown," and MUSM 21112 as "pale brown, almost cream." Lacking specimens of adults, it is not possible to comment further

on variability of this feature or other characteristics. Juvenile and other subadult plumages of other *Poliioptila* species are, however, quite similar to adult plumages (these being basic plumages in the cases of species with different alternate plumage; Ridgway 1904, Atwood and Bontrager 2001). This accords well with our sightings from the field. Food-begging birds in the company of singing adults (i.e., the birds feeding them) show no noticeable plumage differences from adults. Furthermore, adults appear to show no plumage variation through the year, never acquiring any conspicuous areas of black or white (e.g., mask, cap) on the head.

Habitat and behavior.—*Poliioptila clementsii* appears to be uncommon or rare (encountered 0–3 times per week, $n = \sim 50$ observations) in the Allpahuayo-Mishana National Reserve, occurring only in white-sand forest having a variable canopy height of about 15–30 m, and is most consistently present in what local botanists have defined as *varillal alto húmedo* (tall, humid *varillal* forest). These physiognomically simple *varillal* forests were characterized by Whitney and Alvarez (1998) and described in detail by García Villacorta et al. (2003). In *varillales*, canopy height and species composition and abundance of plants, even major groups of plants such as bromeliads and palms, varies over a small spatial scale in accordance with edaphic conditions and drainage properties (e.g., Poulsen and Tuomisto 1996, García Villacorta et al. 2003). Similarly, presence of *P. clementsii* is highly patchy and it appears that considerable areas of seemingly suitable habitat contiguous with active territories are not occupied. Since its discovery, careful searches for *P. clementsii* have been conducted in all forest habitats in northern Loreto by using tape recording playbacks and by observing from the ground with binoculars and telescopes; this has enabled us to define its habitat more specifically than has been possible for most other small, forest-based passerines. We had expected to find *P. clementsii* along the middle and upper Rio Nanay. At two places along the upper Nanay, however, we have found *Poliioptila plumbea* (Tropical Gnatcatcher) accompanying mixed-species flocks in the canopy of *varillal* habitats, occupying the potential ecological space of *P. clementsii*. Within Allpahuayo-Mishana,

P. plumbea is restricted to seasonally flooded forest along the margins of the Rio Nanay.

Tall trees of *Caraipa tereticaulis* and *C. utilis* (Clusiaceae) are among the dominant canopy trees in appropriate habitat, and pairs or small family groups of *P. clementsi* were often seen foraging in these trees (see frontispiece). Palms (Arecaceae) also occur, including the widespread *Euterpe caatinga* and the less common *Mauritia aculeata* and *M. carana*. Arboreal epiphytes are rare. Understory plant composition is also variable, but is typically dominated by some combination of the ferns *Trichomanes martiusii* and *T. bicornis* (Hymenophyllaceae), the herb *Rapatea ulei* (Rapateaceae), and various species of bromeliads, such as *Guzmania lingulata* and *Neoregelia* sp. (Bromeliaceae).

Polioptila clementsi foraged exclusively in the canopy and subcanopy (upper 1/4 of trees) with mixed-species flocks composed primarily of other insectivores and usually including some small frugivores and nectarivores. Attack maneuvers ranged from gleans and short, stabbing reaches to acrobatic chases of fleeing prey as the birds moved lightly and incessantly through the terminal portions of live, leafy branches. All leaf surfaces were checked rapidly. The tail was partially cocked, frequently flicked laterally, and briefly opened slightly to expose the white outer rectrices. (In all these aspects, the foraging behavior of *P. clementsi* appears to be typical for the genus.) These irregular movements may startle small, hidden arthropods into revealing their presence and probably help family members maintain visual contact. The wings were shallowly flicked outward (without opening) almost constantly. This tiny motion may effect a state of readiness for instantaneous pursuit of flushed prey items. Stomach contents of MUSM 21112 contained insect fragments and many small white eggs of an arthropod. One individual that had apparently just bathed was observed sunning itself and preening on a limb for more than 5 min.

Vocalizations.—We have documented with tape recordings six types of vocalizations from *Polioptila clementsi*. The loudsong is a distinctly two-parted series of sharp, thin (unmodulated, no harmonics) notes. It begins with three evenly paced (slow enough to be counted in the field) open, “inverted chev-

rons” peaking at approximately 8 kHz, and then breaks into a much faster, trilled series of evenly paced, nearly vertical notes at just over 6 kHz (Fig. 1A). Loudsongs are usually slightly less than 2 sec in duration, but may exceed 2.5 sec after tape-recording playback; no other features have been observed to change following playback of birds’ own songs or songs of other individuals. We analyzed nine loudsong recordings of *P. clementsi*, most of which consisted of 3–20 or more songs. All songs began with the three introductory notes described above; there was no variation in this character. In fact, the loudsong of all individuals was remarkably consistent in all aspects. At least three clearly recorded songs of each individual were extracted and measured using “Canary” 1.2.4 of the Bioacoustics Program of the Cornell Laboratory of Ornithology (Ithaca, New York). Spectrograms were produced using the default settings and 75% overlap.

Although any number of other features could have been quantified, we selected three independent characters for critical measurement: pace (see below) of the first three notes, pace of the rest of the notes (all those after the first three), and change in peak frequency (Δ PF) from the first to the last note. Measurements for the three songs from each individual were then averaged to obtain a value that reflected some attempt to control for intra-individual variation (Table 2). All measures were made at the scales shown in Figure 1 and at the peak frequency of notes, as this was the only unambiguous point (i.e., permitting easily reproducible results) on these highly vertically oriented spectrogram traces. The “inverted chevrons” of the first three notes were measured this way, as well, to permit appropriate comparison with the first three notes in the songs of some other taxa in the complex. Thus, pace more effectively quantified the time intervals between notes than the duration of the section measured, because, in the case of the first three notes especially, the measurement point hit not the left/right edges of the open chevrons, but the highest point (peak) of the note. Pace of the first three notes in the loudsong was 0.14 sec (range = 0.13–0.16 sec). Pace of the remaining notes was 0.07 sec (range = 0.06–0.07 sec); Δ PF was 1.98 kHz (range = 1.75–2.30 kHz). Both parts of the loudsong

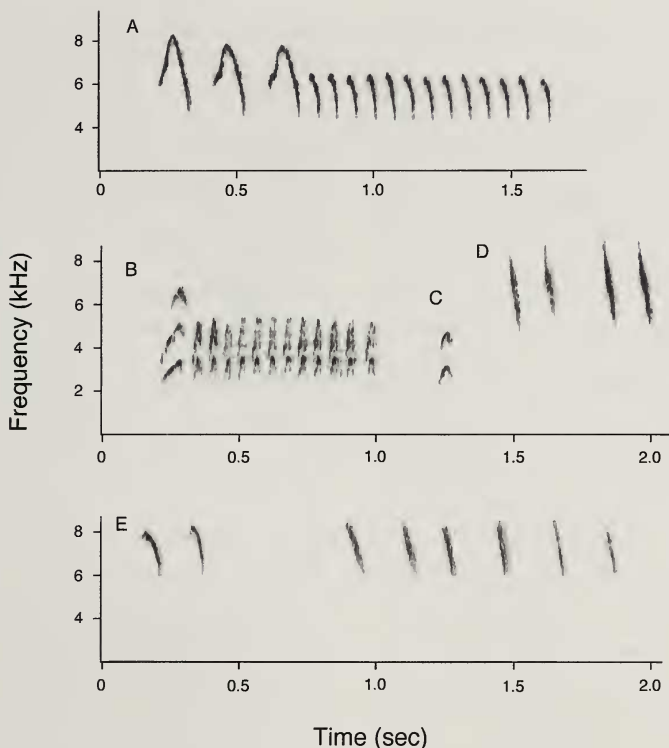


FIG. 1. Sound spectrograms of vocalizations of *Polioptila clementsi*. Recordings are by JAA except as noted. The frequency scale is uniform for all spectrograms, but note that some do not show the area below 4.0 kHz. (A) Typical loudsong showing three distinct introductory notes; all recorded songs were closely similar to this (Table 2); (B) quiet, single-note call with a harmonic heard only a few times; (C) typical multi-note call with emphasis on the introductory note and pronounced harmonics; (D) flight calls, given in doublets (recorded by BMW); (E) irregular series of sharp calls sometimes given while foraging.

were characterized by essentially uniform pace and lack of frequency shifts.

The second most frequently recorded vocalization of *P. clementsi* ($n = 3$ recordings) was a multi-note call lasting 0.5–1.0 sec, sounding like a brief, quiet chatter, in which the first note is distinctly louder and longer, and all notes have harmonics (Fig. 1B). We have not been able to determine its context. Other vocalizations (represented by only one or two recordings) are a quiet, single-note call having a closed “inverted chevron” shape at about 3 kHz that also has a harmonic (Fig. 1C); a sharp call given in flight that makes a straight, nearly vertical trace from about 5.5 to 9 kHz (Fig. 1D); sharp (bent vertical trace) calls structurally similar to notes in the fast section of the loudsong but peaking at about 8 kHz and often given several times in irregular succession while foraging (Fig. 1E); and a food-begging call similar to the call shown

in E but which features a structurally distinct introductory note ahead of a regularly paced series of sharp notes. One additional vocalization was heard once by BMW, but unfortunately it could not be recorded. A singing bird in the company of its mate responded to playback of its own song by flying out of a tree above the trail (about 12 m above ground) and then tightly circling the narrow canopy of the tree one complete turn (360°) while rapidly pumping its tail up and down as it delivered a distinctively cadenced sound—something like *chik-CHEE-dee, chik-CHEE-dee, chik-CHEE-dee, chik-CHEE-dee*. . . . Such flight displays accompanied by a vocalization quite different from the typical loudsong are occasionally given by many species of oscine passerines (BMW pers. obs.). Their function remains obscure, but in this case the display and vocalization clearly resulted from agita-

tion at the presence of a perceived conspecific male intruder.

Intragenetic relationships.—Morphologically, *P. clementsi* is rather weakly differentiated from *P. guianensis*, although it has a longer bill (two-tailed *t*-test, $P = 0.008$), and a diagnostically different tail pattern from the three named taxa in *P. guianensis*, among other more subtle characters revealed in taxon-by-taxon comparisons (see Diagnosis, above). The general structure and steady pace and frequency of its loudsong, and its multi-note call (Fig. 1B), also place *Poliioptila clementsi* firmly in the *P. guianensis* group. The multi-note call with harmonics given by members of the *P. guianensis* complex is unique in the genus (BMW pers. obs.). Thus, *Poliioptila clementsi* is clearly an integral member of the widespread *P. guianensis* complex (which would be called the *P. schistaceigula* complex if that species is considered an allospecies; see below). Considering the fact that another well-studied pair of sister taxa in the genus, *P. melanura* (Black-tailed Gnatcatcher) and *P. californica* (California Gnatcatcher; Atwood 1988, Atwood and Bontrager 2001), are not as well-differentiated phenotypically in either morphologies or vocalizations as *P. clementsi* and *P. guianensis*, we are satisfied that species status is appropriate for both *P. clementsi* and for other taxa currently recognized as subspecies, as discussed below.

REVISION OF THE *POLIOPTILA* *GUIANENSIS* COMPLEX

Morphology.—Zimmer (1942) considered *Poliioptila guianensis* closely related to, and possibly conspecific with, trans-Andean *P. schistaceigula*, and it is primarily for this reason that we have included mention of the latter species in this paper. Neither Zimmer (1942) nor Mayr and Paynter (1964, following Zimmer) provided any justification for this opinion; the relationship was deemed “uncertain” by the American Ornithologists’ Union (1998:494). We do not consider *P. schistaceigula* an allospecies in the *P. guianensis* complex, although we suspect that it is sister to the group. If it is a close relative, it is clear that *P. schistaceigula* has differentiated strongly, both morphologically and vocally, from the much more widely distributed cis-Andean radiation comprising the three named

taxa in *P. guianensis*, and now *P. clementsi*. Differentiation appears to be much less advanced east of the Andes, where several allopatric forms share closely similar morphology (Table 1) and a loudsong template of a rapid series of nearly evenly spaced notes lasting about 1.5–2 sec. The paucity of specimens (especially females) and recordings hamper study of the complex. Furthermore, these small, lightly built birds are difficult to prepare as museum skins; on a few specimens it is not possible to be sure that certain features, particularly the presence and extent of white feathering around the eyes and lores, can be seen sufficiently well to allow meaningful comparisons. However, it seems reasonable at this point to offer a better estimation of taxonomic limits than has been attempted to date. Stotz et al. (1997) provided an accurate overview of some of the characters discussed below. Figure 2 maps the distribution of the *Poliioptila guianensis* complex (nominate *guianensis*, *P. g. facilis*, and *P. g. paraensis*), *P. clementsi*, and *P. schistaceigula* and shows, we believe, virtually all records for all of the taxa (localities within about 50 km are mapped as a single point following Isler 1997).

Tails.—The amount of white and black on the rectrices is slightly variable on all individual birds (i.e., rectrix on one side of the bird shows slightly different extent of white than its counterpart on the other side) and among specimens within taxa; nonetheless, it provides the most salient plumage feature for intertaxon comparisons (i.e., this fluctuating asymmetry is not of sufficient magnitude to confound taxon identifications). Nominate *guianensis* invariably has the most white, with the outer two rectrices entirely white and rectrix No. 4 entirely or almost entirely white. None of the 12 specimens examined (both sexes included), which spanned the entire known range of this taxon, has any white on the three inner pairs. Both *P. g. facilis* and *P. g. paraensis* have considerably more black on the outer three rectrices than nominate *guianensis* and are similar to each other. One of the *facilis* males from Jaú shows two small blotches of white at the tip of No. 3 on the left feather only, and tiny grayish fringes are present at the tip of No. 3 in other *facilis* specimens. Topotypical specimens of *paraensis* (*n*

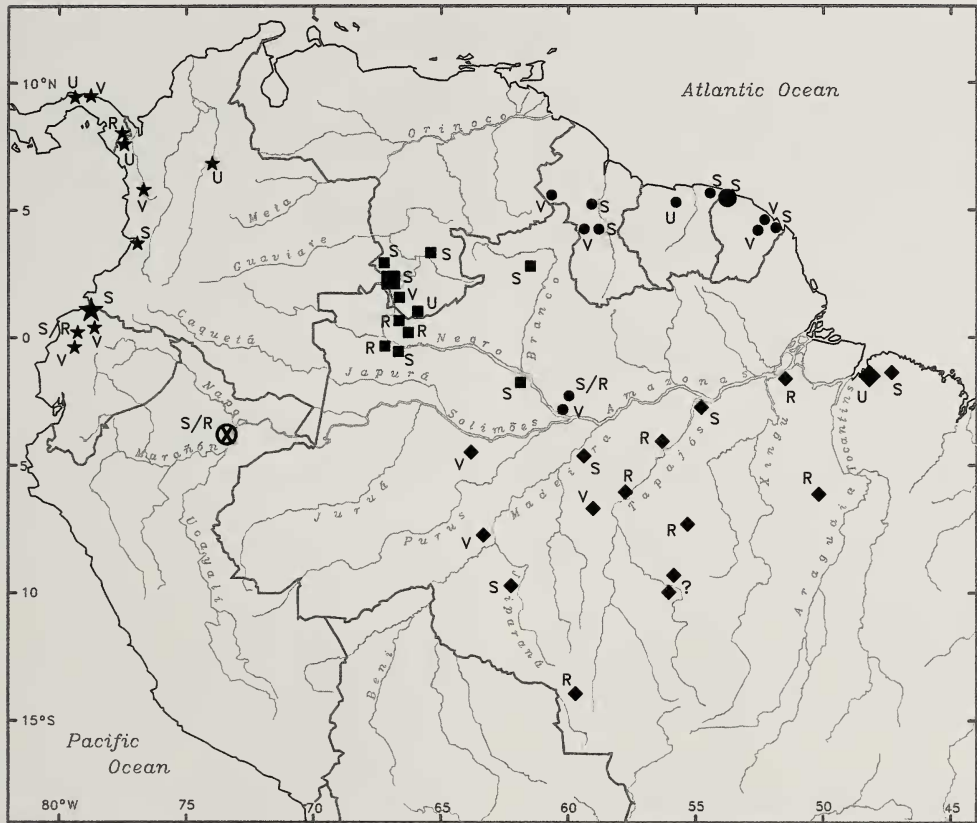


FIG. 2. Distribution of taxa in the *Polioptila guianensis* complex, and that of *P. schistaceigula* (stars). X marks the type locality of *P. clementsi*; dots are *P. g. guianensis*; squares are *P. g. facilis*; diamonds are *P. g. paraensis*. Type localities are enlarged symbols. S beside a symbol means we examined a specimen from that locality; R means we have a recording; U means there is a specimen reported in the literature that we have not examined; and V marks undocumented sight records. The single question mark (?) on the upper Rio Tapajós/Teles Pires marks two or three sight records from opposite sides of the river in the Alta Floresta area, where fieldwork has been extensive but where we still lack confirmation (no specimen, recording, or photo) of occurrence; we hesitate to map these particular records until documentation becomes available. The distance between *P. clementsi* and the nearest known population of *P. guianensis*, on the upper Rio Negro in Brazil, is approximately 800 km.

= 2) have a small white tip (~3 mm) on rectrix No. 4 with no white on the three inner feathers; all other specimens ($n = 4$) show a larger white tip (~6 mm) on No. 4, and a very small (~2 mm) white tip on No. 3. As noted by Zimmer (1942), *P. g. paraensis* tends to have the longest tail of all (Table 1).

Other plumage features.—The throat of all *P. g. guianensis* specimens is slightly to markedly more whitish than the breast, although females show less contrast and are more whitish overall (this seems to be true for all taxa). Males show a narrow but fairly conspicuous, often slightly broken, white eye-ring; females

seem to have a more conspicuous eye-ring and narrow white superciliary, as well. Of the five males from French Guiana, one (CM 61912) has an obvious white supra-oral streak extending to the nares, three show some indication of it (as does the single male from Guyana), and one (CM 61923) has none at all. Among all males of other taxa, none shows any sign of the supra-oral streak. The gray of the plumage of *P. g. facilis* is of about the same tone as that of nominate *guianensis* (Zimmer 1942 considered it a little paler), but the throat of males is nearly concolor with the breast rather than distinctly more whitish, and

facilis has no, or only a hint, of white around the eye. Plumage of *facilis* specimens from the entire range of points mapped in Fig. 2, encompassing both banks of the upper Rio Negro, shows no appreciable variation, but a larger sample is desirable. *Polioptila g. paraensis* is the palest form overall. Like *P. g. facilis*, and unlike nominate *guianensis*, it shows little or no throat-breast contrast. A male and a female from near the type locality show almost no eye-ring; all others show a weak and broken white eye-ring intermediate in contrast relative to those of *P. g. guianensis* and *P. g. facilis*.

Soft-part colors.—Iris color was recorded for eight specimens of *P. guianensis*. All but two of them were recorded as brown or grayish-brown. The adult (skull 100% ossified) female from Rondônia had a “pale gray” iris. Two of the specimens of *P. g. facilis* are noteworthy. FMNH 344215 (male with 90% ossified skull) from Roraima, a short distance west of the Rio Branco, had a “pale yellow orange” iris (label data; Stotz et al. 1997 cited it as “bright orange-yellow”); this was the only brightly colored iris of any specimen in the complex. MPEG 50678 (male with 100% ossified skull) from west of the middle Rio Negro in Jaú National Park had a “brown” iris. Determination of whether these quite different eye colors from localities on opposite banks of the Rio Negro have any geographic restriction awaits further collection of specimens and perhaps careful observations in the field. No differences in the coloration of bills, legs, or feet were noted among taxa, but data from collectors/preparators are generally lacking.

Vocalizations.—Figure 3 shows loudsong spectrograms of the members of the *Polioptila guianensis* complex. Measurements of the characters described for vocalizations of *Polioptila clementsii* (above) are summarized by taxon in Table 2. We have illustrated examples from fairly near type localities (mapped in Fig. 2) for *P. g. facilis* and *P. g. paraensis*, but unfortunately we have no recordings of *P. g. guianensis* from near the type locality in French Guiana. However, our examples from near Manaus, Amazonas, Brazil come from the same localities as specimens that are phenotypically almost identical

to the several paratypes of nominate *guianensis*.

The loudsong of *Polioptila g. guianensis* (Fig. 3A; $n = 2$) appears to be a simple, evenly paced repetition of a thin, sharp “inverted chevron” note with greater intensity on the left side of the note. It is also quite level in frequency, with a ΔPF of 0.47 kHz. The loudsong of *P. g. facilis* from the left (north) bank of the upper Rio Negro (Fig. 3B; $n = 4$) has the highest introductory note of any of the taxa (~ 9 kHz); a slightly lower second note is often coupled with it, followed by the rest of the series at a steady, slower pace slightly above 8 kHz. Notes in the series are “inverted U” traces. The song of one individual was more evenly paced throughout (no coupling of the first two notes) with the series at about 7 kHz; ΔPF north of the Rio Negro was 0.94 kHz including this individual. Directly across the upper Negro, the first note of the song peaks at about 7 kHz and ΔPF is 0.64 kHz ($n = 2$); pace and note shape appear to be essentially the same as they are in songs of birds from the north bank of the river. The “inverted U” notes of *facilis* have highest amplitude at the peak, with nearly equal intensity on the arms; this, together with the rounded shape of the peak of notes in the series, gives the song a slightly softer quality than those of other taxa.

Measures for the loudsong of *P. g. paraensis* (Table 2) were restricted to the sample from the Caxiuanã National Forest west of Belém because this is fairly near the type locality and we had several recordings from there. It is a simple, steadily paced repetition of a sharp, “inverted chevron” note having greatest intensity on the right side (Fig. 3C). Peak frequency range is nearly flat, with ΔPF of only 0.37 kHz.

Discussion.—All three named taxa in *Polioptila guianensis* differ diagnostically from *P. clementsii* and from each other in both plumage and voice. Published subspecies divisions based entirely on morphological traits accord well with differences in vocalizations, and levels of phenotypic differentiation in the complex seem approximately equivalent. In spite of small sample sizes for most members of the group, we are confident that individual specimens and tape recordings of loudsongs can be assigned unequivocally to taxon as cur-

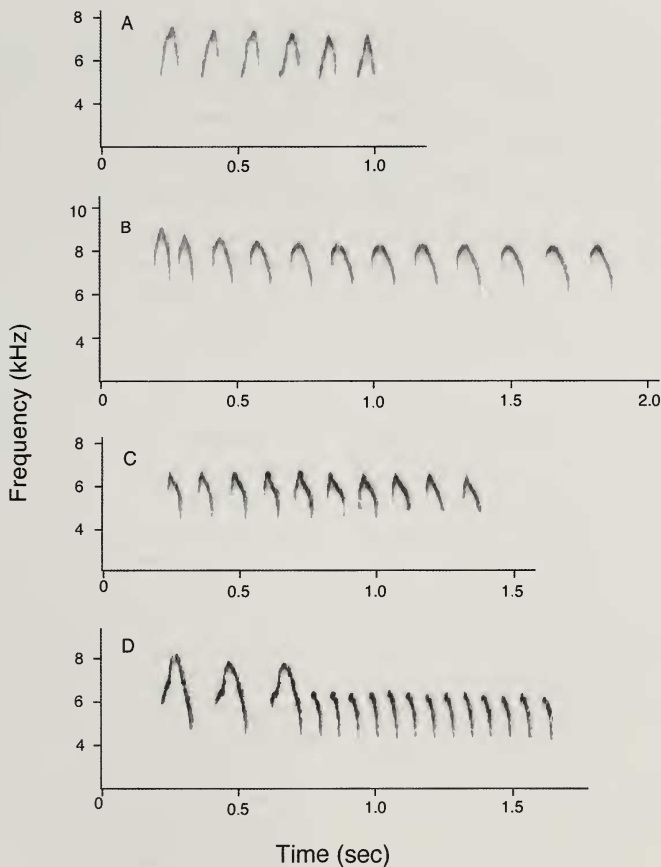


FIG. 3. Sound spectrograms of loudsongs of members of the *Polioptila guianensis* complex. The frequency scale is uniform for all spectrograms, but the area below 4.0 kHz is omitted. (A) *P. g. guianensis* from near Manaus, Amazonas, Brazil; intensity is greatest on the left side of the “inverted chevron” notes; recorded by L. Naka; (B) *P. g. facilis* from 17 km north São Gabriel da Cachoeira, left (north) bank of the upper Rio Negro, Amazonas, Brazil, ~300 km south of the type locality; the “inverted U” notes of *facilis* are distinctive; recorded by K. J. Zimmer; (C) *P. g. paraensis* from the Caxiuanã National Forest, ~400 km west of the type locality; recorded by BMW (D) *P. clementsi* from the type locality (same spectrogram as Fig. 1A); recorded by JAA.

rently defined. Vocalizations may represent a more reliable character set than morphology for distinguishing some forms. Atwood and Bontrager (2001) reached the same conclusion with regard to identification of *Polioptila melanura* and *P. californica*, two narrowly syntopic sister-species (Zink and Blackwell 1998). As an oscine passerine assemblage, however, the question of whether vocalizations can be expected to reflect evolutionary divergence, as they have proven to do quite accurately in the cases of some subsocine passerine groups (Arctander and Fjeldså 1994, Cohn-Haft 2000), should be addressed.

It has been shown for several species of oscine passerines that some elements of songs

are learned during some “critical period” (apparently often the nestling stage), which, subject to a variety of circumstances, can lead to geographically restricted dialects. In a study of the Rufous-collared Sparrow (*Zonotrichia capensis*) in northern Argentina, Loughheed et al. (1993) reported that mtDNA variation observed along a 50-km transect crossing three well-documented song dialects was overlain by, but unrelated to, these dialects. They went on to suggest that “cultural evolution resulting in dialects does not affect dispersal or mating patterns, and, thus, does not promote genetic differentiation.” Looking at a greatly expanded area of coverage, however, they concluded that “hyperdiverse mtDNA and al-

lozyme characters together provide preliminary evidence of large-scale patterns corresponding to subspecies divisions. . . .” Thus, macrogeographic sampling of vocalizations of a widespread oscine passerine seems an appropriate starting point for evaluating the taxonomic ranking of named taxa (i.e., morphologically distinct forms) as well as identifying unnamed populations.

The meager sample of recordings of *P. g. guianensis* was limited to the Manaus area, so it was not possible to investigate whether any geographic structure in vocalizations might be present within its range. Our recordings of *P. g. facilis*, from opposite banks of the upper Rio Negro, show quite similar pace and note shapes, but somewhat different Δ PF owing primarily to the higher, sharper introductory note given by birds on the left (north) bank. The upper Negro may separate different dialects or, more likely, we believe it represents a maintenance barrier for genetic divergence as it does for some *Hemitriccus* flycatchers (Cohn-Haft 2000) and other groups of birds. The only taxon for which we have samples from a wide area is *P. g. paraensis*, which shows little variation in the region between the Tapajós and Tocantins rivers.

It is important to note that loudsongs of members of the *P. guianensis* complex from localities for which we have several recordings (*P. clementsi* near Iquitos; *P. g. paraensis* at Caxiuanã) show remarkable consistency in all characters measured, as well as important qualitative attributes, such as note shape and tonality. In fact, ranges of measures (Table 2) are quite similar to those reported for larger samples of some thamnophilid antbirds (Whitney and Alvarez 1998; Isler et al. 1999, 2002). We expect that other taxa in the complex will prove to show similar, low levels of variability in their vocalizations. In sum, the evidence points to a lack of any learning element in the development of songs and calls in the *P. guianensis* complex. Similarly, Atwood and Bontrager (2001) concluded that learning is likely not a factor in vocal development in *P. californica*.

The potential to learn some elements of song does not exclude the possibility, or even probability, that vocal templates of oscines are a phenotypic expression of genetic determination and are thus potentially informative in

taxonomic and systematic study. Capacity for song learning and the actual extent of learning of vocalizations have not been studied for any forest-based Neotropical oscine passerine. Extensive field work in most areas of the Amazon basin and other primarily forested habitats in South America indicates to us that, like members of the *Polioptila guianensis* complex, some oscine passerines as unrelated as *Microcerculus* wrens and *Hylophilus* greenlets have maintained a high degree of uniformity of vocalizations across broad geographic fronts, yet show marked geographic differentiation, in accordance with patterns observed for numerous suboscine species (BMW pers. obs.). Another widespread complex in the genus *Polioptila* that shows significant geographically structured variation in morphology, vocalizations, and habitat specificity is the *P. plumbea* group (BMW pers. obs.), but it has not yet been studied.

Taxonomic conclusions.—Until we have sufficient data to offer a different, or more complete, picture of speciation in the *Polioptila guianensis* complex, and in consideration of the similar or lesser levels of phenotypic differentiation documented for some other sister-species complexes in the genus, we propose that *Polioptila clementsi* and the three subspecies of *Polioptila guianensis* henceforth be recognized at the species level (this complex probably sister to *P. schistaceigula*) with the following names:

Polioptila guianensis, Guianan Gnatcatcher
Polioptila facilis, Rio Negro Gnatcatcher
Polioptila paraensis, Para Gnatcatcher
Polioptila clementsi, Iquitos Gnatcatcher

Both *P. guianensis* and *P. facilis* are known from the left (east) side of the Rio Negro, and the latter has been collected (one specimen) in Roraima a short distance west of the Rio Branco. We suspect that the Rio Branco separates these two forms; this region, however, remains among the most undersampled areas of Amazonia. Similarly, the vast region between the Manaus area and the three Guianas (Fig. 2) has seen almost no collecting; we expect that all forested areas in that hiatus are occupied by *P. guianensis*. In this study, all specimens from south of the Amazon River are provisionally called *P. g. paraensis*. Although linked by pale coloration and long

tails, they are few ($n = 6$) and widely scattered (Fig. 2). For example, we have little information from west of the Rio Tapajós and only two sight records from anywhere west of the Rio Madeira (one of these reported by Peres and Whittaker 1991). We predict, however, that an undetected population inhabits most of the region west of the Madeira north of about 7° S, west to Peru; it should be sought especially in forests growing on white sand and extensively weathered clays (both patchily distributed *terra firme* habitats). There are many additional gaps on the map, and clearly much more work will be required to gain an accurate understanding of how members of the *P. guianensis* complex are distributed. Collection of additional specimens and tape recordings from poorly known areas of the distribution of the *Polioptila guianensis* complex may soon confirm the existence of one or more additional, unnamed populations of these obscure, Neotropical forest gnatcatchers.

As a final thought, in the only study to date that addresses the way in which molecular evolution informs species relationships within the genus *Polioptila*, Zink and Blackwell (1998) reported an mtDNA sequence divergence of about 4% between the sister-species *P. melanura* and *P. californica*. We expect that the level of sequence divergence among members of the *P. guianensis* complex could vary considerably from this owing to a variety of factors such as much larger population sizes of most taxa, evolution in far more stable environments and, probably, lower reproductive rates and increased longevity. Thus, a level of divergence deemed appropriate for recognition of taxa at the species level in one region of the world may not necessarily find its equivalent for obviously related taxa that have evolved in radically different environments. Molecular analysis of the widespread *Polioptila guianensis* group may have the potential to illuminate speciation patterns applicable to a variety of forest-based Amazonian birds.

CONSERVATION

The discovery of *Herpsilochmus gentryi* and other species (not only birds, but other vertebrates and plants) new to science or new to Peru, led the Instituto de Investigaciones de la Amazonía Peruana (IIAP) to propose to the

Instituto Nacional de Recursos Naturales (INRENA) the creation of a reserve to protect the rare white-sand habitats near Iquitos. On 16 January 2004, the status of Zona Reservada Allpahuayo-Mishana (established 4 March 1999) was elevated to the Reserva Nacional Allpahuayo-Mishana, encompassing 58,070 ha and protecting the greatest known concentration of white-sand habitats in the Peruvian Amazon. The entire known range of *Polioptila clementsii* is officially protected. However, its presence is confirmed from only about six localities in an area of no more than 2,000 ha because appropriate *varillal* forest is highly patchy in distribution. We estimate that a maximum of 50 pairs survive in the reserve.

Over the past 3 decades, a high percentage of the once-extensive *varillal* habitats in and surrounding the known distribution of *Polioptila clementsii* has been fragmented or destroyed as the Peruvian government encouraged colonization of the area near Iquitos. Agricultural initiatives have largely failed on these nutrient-deficient, quartzitic soils, yet persistent colonists have cleared the land, selling the long, straight trunks of *varillal* trees for construction, firewood, and making charcoal, which, within a national reserve, is prohibited by Peruvian law (Fig. 4). Today, the only known population of *Polioptila clementsii* is fragmented into three parcels separated primarily by deforested terrain. Titled landholders who live within the reserve area take a daily toll on the habitat; destruction is especially accelerated near the paved highway linking Iquitos with the town of Nauta. In mid-2004, the municipality of San Juan (on the west edge of Iquitos) rapidly opened a clandestine road, ostensibly to "promote tourism," along the northern edge of the reserve in an area occupied by several pairs of *P. clementsii*; this is sure to result in significantly increased habitat destruction in this heretofore pristine area. Fragile and highly vulnerable climax *varillal* forests may never properly regenerate from fragmentation because they grow on such nutrient-poor soils. In fact, the place in the reserve in which the specific habitat of *Polioptila clementsii* receives the best protection is the property of the Instituto de Investigación e Extensión Agraria near Km 25 (El Dorado), where the species was discov-



FIG. 4. Destruction of the extensive *varilla* forest, prime habitat of *Polioptila clemensi*, at Nueva Esperanza in the Reserva Nacional Allpahuayo-Mishana near Iquitos, Loreto, Peru. The long, straight trunks of the dominant trees in this habitat, such as *Caraipa tereticaulis*, are easily cut for construction, firewood, and making charcoal. These ancient and slow-growing forests occur on especially nutrient-poor, quartzitic soils, and may never be able to regenerate. Photo by JAA, September 1998.

ered. Illegal extraction of timber continues even there.

Considering its very small, habitat-specialized world population, the great reduction of appropriate habitat in the recent past, and the continuing destruction of existing habitat, we recommend that *Polioptila clemensi* be classified as Critically Endangered. We are optimistic about its preservation within the Reserva Nacional Allpahuayo-Mishana, as much-needed funding is now being channeled directly to the preservation effort administered by IIAP in Iquitos. J. D. Alvan, an enthusiastic and highly skilled young ornithologist, has been hired to carry out field research on *Polioptila clemensi* and to initiate local environmental education programs in the Iquitos area. Park guards will receive dependable salaries; boats and motors will be provided to, and maintained for, cooperative communities along the Rio Nanay; fuel will be purchased; and goods will be distributed.

These simple but critically important aspects of the reserve's preservation have been made possible by the generous monetary contribution of James F. Clements. The challenge will be to maintain funding levels far into the future. Threats to the habitat are increasing just as every year brings more exciting discoveries of plants, insects, amphibians, and other organisms new to science from the white-sand forests of Allpahuayo-Mishana and the Rio Nanay.

The attractive Spanish name "Perlita de Iquitos" (Little Pearl of Iquitos) has inspired Mayor Juan Carlos Del Aguila Cardenas and the Provincial Municipality of Maynas council to adopt the gnatcatcher as the official bird of the city. La Perlita de Iquitos will be used in educational and promotional programs as a symbol of the city's commitment to the bird's conservation and protection of its fragile habitat and the surrounding region.

ACKNOWLEDGMENTS

JAA is grateful to Flora and Fauna International—100% Fund (Cambridge, UK) and Bergstrom Awards of the Association of Field Ornithologists (Houston, USA), both of which supported field research in 1998 and 1999. Idea Wild (USA) generously donated mist nets. The Dirección General de Areas Naturales Protegidas y Fauna Silvestre—INRENA provided necessary permits for study and specimen collection in the Zona Reservada Allpahuayo-Mishana. We appreciate the assistance of R. Panza, M. LeCroy, P. Sweet, C. Blake, D. Willard, S. J. Hackett, J. M. Bates, L. Joseph, N. Rice, J. V. Remsen, and S. Cardiff for loaning specimens. I. Franke was especially helpful with our work at MUSM. We are grateful to the recordists C. A. Marantz, L. Naka, J. F. Pacheco, A. Whittaker, and K. J. Zimmer for sending us copies of their recordings of *P. guianensis*, and to C. Bauer for help with copying some of BMW's recordings. A. Whittaker also helped JAA collect one of the *P. clemensi* specimens. We thank J. C. Ruiz for identifying many plant specimens. M. L. Isler kindly prepared the map for Figure 2. J. V. Remsen made helpful editorial changes and provided a sounding board for some of the discussion on taxonomic revision. D. F. Stotz and two anonymous reviewers provided insightful suggestions for improving the manuscript. BMW is grateful to Field Guides, Inc. of Austin, Texas, which partially supported fieldwork, and to the many tour co-leaders and participants who have helped him make tape recordings and other gnatcatcher observations in South America. We thank J. Icomena and E. Aquituarí, dedicated and helpful park guards of the Allpahuayo-Mishana Reserve. Finally, we are grateful to L. McQueen for his excellent portrayal of the Iquitos Gnatcatcher in habitat, which is the frontispiece for this issue.

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